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de la Malla, C.; Lopez-Moliner, J.; Brenner, E.

published in
Journal of Vision
2014

DOI (link to publisher)
10.1167/14.12.8

document version
Publisher's PDF, also known as Version of record

Dealing with delays does not transfer across sensorimotor tasks

Cristina de la Malla
Vision and Control of Action Group, Departament de Psicologia Bàsica, Universitat de Barcelona, Catalunya, Spain
Institute for Brain, Cognition and Behaviour (IR3C), Barcelona, Catalunya, Spain

Joan López-Moliner
Vision and Control of Action Group, Departament de Psicologia Bàsica, Universitat de Barcelona, Catalunya, Spain
Institute for Brain, Cognition and Behaviour (IR3C), Barcelona, Catalunya, Spain

Eli Brenner
MOVE Research Institute Amsterdam, Faculty of Human Movement Sciences, VU University Amsterdam, Amsterdam, The Netherlands

It is known that people can learn to deal with delays between their actions and the consequences of such actions. We wondered whether they do so by adjusting their anticipations about the sensory consequences of their actions or whether they simply learn to move in certain ways when performing specific tasks. To find out, we examined details of how people learn to intercept a moving target with a cursor that follows the hand with a delay and examined the transfer of learning between this task and various other tasks that require temporal precision. Subjects readily learned to intercept the moving target with the delayed cursor. The compensation for the delay generalized across modifications of the task, so subjects did not simply learn to move in a certain way in specific circumstances. The compensation did not generalize to completely different timing tasks, so subjects did not generally expect the consequences of their motor commands to be delayed. We conclude that people specifically learn to control the delayed visual consequences of their actions to perform certain tasks.

Introduction

We are often exposed to delays between our actions and their (visual) consequences. Such delays are becoming ever more prominent with the increasing reliance on electronic devices rather than mechanical tools. People seem to have little difficulty in coping with such delays. When timing is not critical, delays may simply be tolerated (van Mierlo, Brenner, & Smeets, 2007), but there are tasks for which timing is critical.

Adaptation and transfer of adaptation have been observed in tasks in which perceptual judgments were evaluated after manipulating the delay between discrete actions (button presses) and their perceptual consequences (e.g., Heron, Hanson, & Whitaker, 2009; Keetels & Vroomen, 2012; Rohde & Ernst, 2013; Stetson, Cui, Montague, & Eagleman, 2006; Sugano, Keetels, & Vroomen, 2010). It is less clear whether temporal adaptation occurs when performing continuous visually guided movements with delayed feedback. Some studies claim that there is little or no adaptation to delays in such tasks (e.g., Held, Efstathiou, & Greene, 1966; Smith, McCrary, & Smith, 1962; Smith, Wargo, Jones, & Smith, 1963), while others did find some adaptation to delayed visual feedback (e.g., Botzer & Karniel, 2013; Cunningham, Billock, & Tsou, 2001a; Cunningham, Chatziastros, von der Heyde, & Bülthoff, 2001b; de la Malla, López-Moliner, & Brenner, 2012; Kennedy, Buehner, & Rushton, 2009; Rohde, van Dam, & Ernst, 2014; Vercher & Gauthier, 1992). One reason why adaptation may not always be

Citation: de la Malla, C., López-Moliner, J., & Brenner, E. (2014). Dealing with delays does not transfer across sensorimotor tasks. *Journal of Vision, 14*(12):8, 1–17, http://www.journalofvision.org/content/14/12/8, doi:10.1167/14.12.8.

doi: 10.1167/14.12.8 Received January 28, 2014; published October 9, 2014 ISSN 1534-7362 © 2014 ARVO

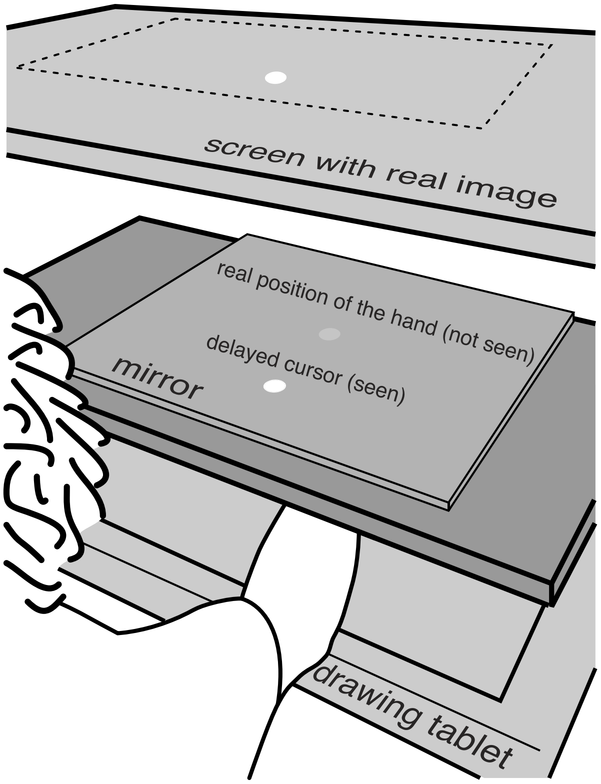

Figure 1. Schematic representation of the setup. The starting position, the target, and a cursor representing the position of the hand were projected on a screen above a half-silvered mirror. The cursor indicated the hand's position after a delay and it was not always visible.

found is that people may adjust their actions to the delay in a manner that does not involve adapting to it. For instance, if there is no time constraint, people may move slowly to reduce the spatial consequences of the delay or may perform multiple brief movements instead of a single continuous movement to avoid relying on feedback during the movement (e.g., Held et al., 1966; Kalmus, Fry, & Denes, 1960; Sheridan & Ferrel, 1963; Smith et al., 1962, 1963). Such adjustments will reduce the consequences of the delay and, thereby, probably the extent of adaptation (Welch, 1978).

Two methods have been used to successfully demonstrate temporal adaptation to delayed feedback for continuous visually guided movements. Cunningham et al. (2001a) and Kennedy et al. (2009) compared performance before and after exposure to temporal delays, whereas Botzer and Karniel (2013) and Cunningham et al. (2001b) also examined the transfer of adaptation to different movements. Whereas the former method will reveal any form of adaptation, the latter will reveal only adaptation that involves processing that is common to the two tasks. We combine both methods to try to unravel the mechanisms of adaptation to delayed feedback about one's own actions in an interception task. Doing so involves examining transfer to other tasks that require temporal precision, but with different goals and movements. We find that subjects successfully compensate for delays of up to at least 200 ms but that such compensation does not generalize well to new tasks. We suggest that subjects learn to control the feedback on the basis of which success is evaluated rather than generally adapting to a new temporal relationship between motor commands and their consequences.

Materials and general methods

Apparatus

Subjects sat in front of a drawing tablet (WACOM A2) that recorded the position of a hand-held stylus at 200 Hz. Stimuli were projected at a frame rate of 85 Hz and a resolution of 1024 by 768 pixels onto a horizontal back-projection screen (InFocus DepthQ Projector, Lightspeed Design, Bellevue, WA) positioned above the tablet (Wacom A2, Wacom, Krefeld, Germany) (Figure 1). A half-silvered mirror between the back-projection screen and the tablet hid the subject's hand from view and reflected the visual display, giving subjects the illusion that the stimuli were on the tablet. For calibration only, lights situated between the half-silvered mirror and the tablet were turned on so that subjects could see the stylus in their hand. The setup was calibrated by aligning the tip of the stylus with dots that appeared on the screen. This allowed us to later present visual stimuli at any desired position on the tablet. Subjects intercepted the virtual targets by sliding the stylus across the drawing tablet. A computer controlled the presentation of the stimuli and registered the position of the stylus.

Subjects

A total of 28 subjects (21 females, seven males) participated in the experiments after giving written informed consent. Most of the subjects took part in more than one experiment. All subjects had normal or corrected-to-normal vision, and none had evident motor abnormalities. They could adjust the height and the position of a chair to ensure they felt comfortable during the experiments. The study was part of a program that was approved by the local ethical committee.

General procedure

In almost all the experiments subjects had to try to hit a moving target with delayed visual feedback about their movement. The target that they were trying to hit was an 8-mm-diameter white dot that could move across the screen either from left to right or from right to left at either 20 or 30 cm/s. For each speed and direction of motion, the target could appear at one of two different distances from the vertical midline of the display. The positions at which the moving target could appear were chosen so that the target would reach the center of the display after either 600 or 700 ms. There were an equal number of trials for each of the eight combinations of initial target position, direction of target motion, and speed of target motion. These trials were presented in a semirandom order (each was presented once before the first was presented twice, and so on, but within each group of eight presentations the order was completely random).

To start each trial (except in the last experiment), subjects had to move the tip of the stylus (which we refer to as the hand) to an indicated starting position (a 5-mm-diameter blue dot that was 10 cm closer to the subject than the screen center, if not mentioned otherwise). A trial started once the hand was within the starting point for a random interval between 300 and 500 ms. At that moment, the starting point disappeared and the moving target appeared. The target's path was 10 cm farther from the subject than the screen center (thus 20 cm farther away from the subject than the starting point, unless mentioned otherwise). Subjects could rest whenever they liked by not placing the hand at the starting position.

The subjects' aim was to intercept the moving target. They were asked to move through it, not to stop on (or ahead of) it. They were free to decide when to start moving and where to hit the target, but they were required to perform a continuous movement without lifting the stylus off the tablet. Subjects could not see their hand or the stylus. During the attempts to hit the target subjects sometimes received visual feedback about the position of their hand. Visual feedback consisted of a 5-mm-diameter white dot (which we refer to as a cursor) that reproduced the movement of the hand. This feedback was delayed by between 60 and 219 ms (our setup has a minimum delay of 60 ms; de la Malla et al., 2012). Details of the methods and procedure that are specific to each of the experiments are provided at the beginning of each experiment's description below. All comparisons of performance before and after adaptation were conducted with paired *t*-tests.

Temporal error

When faced with the task of hitting a moving target with a cursor that is delayed with respect to the movement of one's hand (which itself is not visible), one must move in anticipation of the delayed feedback from the cursor in order to successfully hit the target with the cursor. The temporal error, in terms of when the unseen hand crosses the target's path, can be used as a measure of the degree of adaptation to the delay. If people do not learn to move differently so that the (unseen) *hand* hits the target, the temporal error will be zero. If they fully adapt to the (delayed) visual feedback so that the *cursor* hits the target, the temporal error will be equal to the imposed delay. In our figures we therefore present the temporal error together with a line indicating the imposed delay.

Experiments and results

Experiment 1

In this first experiment we examined how people deal with different kinds of delayed visual feedback about their own movements in an interception task.

Procedure of Experiment 1

We compared performance in three sessions with different kinds of feedback. In one session, subjects saw the cursor following the hand throughout the movement (*full feedback*). The cursor indicated where the hand had been some time earlier. In another session, they saw the cursor only during the final 33% of its trajectory toward the target (including seeing the cursor cross the target's path; *late feedback*). In the final session, the position at which the delayed cursor would have crossed the target's path was displayed together with the target's position at the time that it would have done so. This was shown until the hand moved half way back to the starting position (*spatial feedback*).

In the full feedback session subjects could speed up or aim farther ahead of the target if they saw that they were going to miss the target due to the delay. In the late feedback session subjects could not correct the ongoing movement because the feedback was presented only after the last moment at which they would still be able to respond before passing the target (due to sensory-motor delays), and often even only after the hand had crossed the target's path (due to the added delays between the hand and the cursor). In the spatial feedback session subjects never directly experienced the delay between the hand and the cursor. Between attempts to hit the target, the cursor appeared at the (delayed) position of the hand to help guide the hand back to the starting position, but only when the (delayed) hand was completely static (moved $<$0.5 mm in 50 ms). Thus, even when returning to the starting

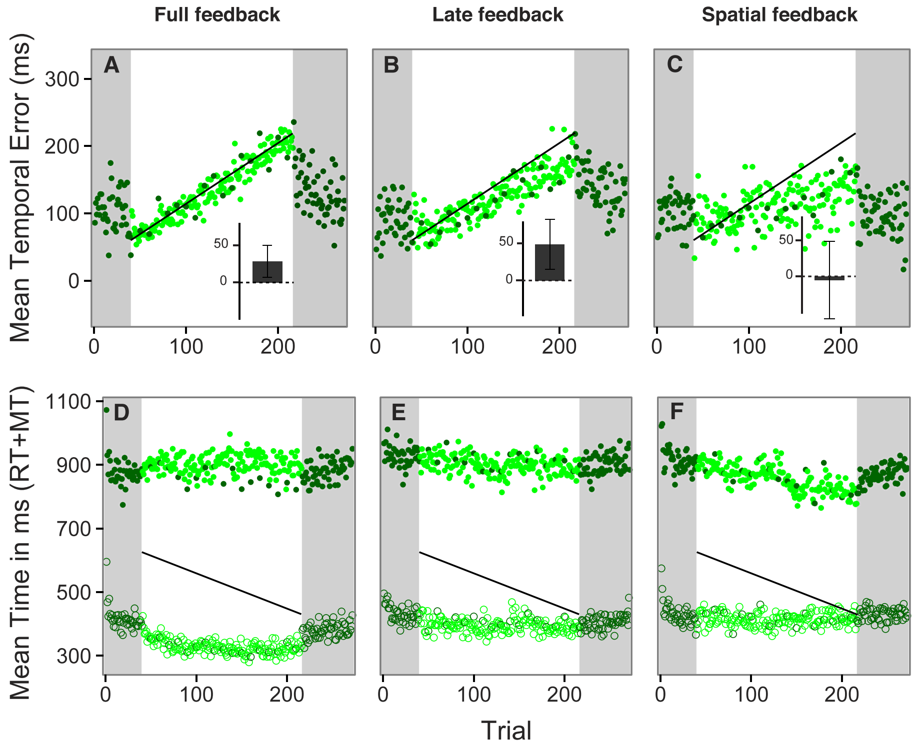

Figure 2. Results of Experiment 1. (A–C) Mean temporal errors: how much earlier than the target the hand crossed the point at which it crossed the target's path (averaged across subjects for consecutive trials). The dark green dots represent trials without feedback. The light green dots represent trials with delayed feedback. The black line shows the temporal error that would make the cursor precisely hit the target. The gray areas indicate blocks of trials without feedback. Each panel represents a different feedback condition. The black bars show the differences between the mean temporal errors in the post- and preadaptation trials (with their 95% confidence intervals). (D–F) Average time at which the hand started to move (open symbols) and at which it reached the target's path (solid symbols), measured from the moment the target appeared, for each condition. Each point is the mean of the nine subjects' values. The black line shows when the hand would have to reach the point on the target's path that is midway across the surface (closest to the starting point) in order for the cursor to hit the target.

position, both whether the cursor was drawn and where it was drawn were influenced by the delay.

Each session started with 40 trials and finished with 56 trials with no visual feedback at all when intercepting the targets. Between these blocks of trials without visual feedback, the delay in the feedback gradually increased from the minimum delay of 60 ms to a delay of 219 ms, at 1 ms per trial. The delay was increased gradually to avoid sudden changes that may make people move in strange ways (Honda, Hirashima, & Nozaki, 2012). Interleaved with the trials with an increasing delay were trials in which subjects received no feedback (every ninth trial). The delay in presenting the static cursor when returning to the starting position was always identical to the last presented delay in interception trials with feedback. It was 60 ms for the first block of trials without feedback and 219 ms for the final block of trials without feedback. In total, each session consisted of 272 trials and took about 20 min to complete. The three sessions were performed on different days in counterbalanced order. Nine subjects (seven females) took part in the experiment.

Results of Experiment 1

Figure 2A through C shows the mean temporal error of the hand as a function of trial number for the three different types of visual feedback. Figure 2A shows temporal errors when subjects had full (delayed) visual feedback of their movement. Such feedback allows them to correct movements online and to experience the altered temporal relationship between the hand and the cursor. Figure 2B shows temporal errors when subjects received visual feedback only from when the cursor had moved two-thirds of the distance to the target's path. By then there was not enough time to correct movements online on the basis of visual feedback, but subjects did experience the temporal relationship between movements of the hand and of the cursor, so they could adjust subsequent movements. Figure 2C shows temporal errors when subjects received static feedback about the spatial extent of their error after each trial but never directly experienced the delay between the hand and the cursor.

All three conditions started with preadaptation trials and ended with postadaptation trials that were performed without visual feedback. There were also some trials without feedback interleaved among the feedback trials. Bright dots represent trials with feedback and dark dots represent trials without feedback. The black line shows the increasing delay that we introduced between the hand and the cursor. For full adaptation, so that the delayed cursor hits the target, the dots will be near this line.

Subjects adapted to the increasing delay when they had feedback throughout the cursor's movement (Figure 2A). In trials with full feedback, if subjects failed to anticipate the delay and therefore started to move too late, they could compensate for this by speeding up or aiming farther ahead of the target. However, their performance in the interleaved trials without visual feedback shows that they did anticipate the delay because the temporal errors on the interleaved trials without feedback follow the black line as closely as the temporal errors on the trials with feedback. When visual feedback was absent for multiple trials (postadaptation trials), the temporal error gradually returned to its original level (see preadaptation trials). Despite this, the difference between the mean temporal error after and before adaptation (black bar in the inset of Figure 2A) is significant ($t_8 = 3.1$, $p = 0.02$).

Adaptation was almost as clear when feedback was presented during only the last part of the movement (Figure 2B). The slightly more variable temporal errors in this condition compared with the full feedback condition are probably the result of it being impossible to make online corrections. Doing so is impossible because by the time the cursor appears, the hand has almost reached (<100 ms remaining) or has already crossed (for the larger delays between hand and cursor) the target's path. The adjustments to the errors are also slightly less complete: They follow the black line less closely than when full feedback was provided. The difference between the mean temporal error after and before adaptation (black bar in the inset of Figure 2B) is significant ($t_8 = 3.3$, $p = 0.01$).

Although this may give the impression that subjects mainly use feedback about their success to adjust their next movement, this is not so because displaying the spatial error immediately after each trial gave rise to much more modest adjustments (Figure 2C). In that case, the difference between the mean temporal error after and before adaptation (black bar in the inset of Figure 2C) was not significant ($t_8 = -0.21$, $p = 0.84$). Thus, perhaps not surprisingly, it seems that the more subjects experience the temporal delay between movements of the unseen hand and movements of the cursor, the more they adapt to the delay. The next experiments examine whether it is this relationship that subjects are learning.

In order to deal with the delay, subjects could start moving earlier, move faster, or aim some distance ahead of the target (either directly or by following a more curved path). Figure 2D through F shows how long after the target appeared the hand started moving (reaction time; open symbols) and how long after the target appeared the hand reached the target's path (sum of reaction and movement time; solid symbols). The black lines indicate the average sum of the reaction time and movement time for which the target would be hit if the hand passed through the target's path at the closest position to the starting point (centered laterally within the setup). That the solid symbols are above the black lines indicates that subjects hit the targets after they had passed the midline.

For the full feedback (Figure 2D) and late feedback (Figure 2E) conditions, the sum of the reaction time and the movement time (solid symbols) does not change systematically across trials. The difference between the time the movement takes in the first nine trials with feedback and in the last nine trials with feedback is not significant in either of these conditions ($t_8 = 0.02$, $p = 0.98$ and $t_8 = 1.33$, $p = 0.22$, respectively, for the full and late feedback conditions; we considered groups of nine trials to include each kind of trial once). That means that subjects aimed farther ahead of the targets in order to deal with the delay, so that the cursor hit the targets when they were farther along their path, while the hand reached the path at about the same time as it did without delays.

In the full feedback condition, the reaction time decreased when feedback was provided and increased again when it was removed. Although starting to move earlier could help compensate for the added delay, this adjustment was counteracted by a longer movement time, so that the total time did not change. The longer movement time is partly due to the hand moving more slowly and partly to it taking a longer path to the target. The average peak velocity of the hand was lower during the last nine trials with feedback (62 cm/s; trials with the smallest delays) than during the first nine trials with feedback (68 cm/s; trials with the longest delays), although this difference was not significant ($t_8 = 1.54$, $p = 0.17$). In order to hit the target with the *delayed cursor* without decreasing the time from when the target appeared to when the *hand* reached the target's path, subjects had to aim for a position farther along the target's path as the delay increased. Consequently, the mean position at which subjects tried to hit the target is significantly farther along its path during the last nine trials with feedback than during the first nine trials with feedback ($t_8 = 5.85$, $p = 0.001$).

Subjects did not start to move earlier in the *late feedback* condition, in which starting to move earlier could also compensate for the added delay, so they probably started moving earlier in the *full feedback* condition in order to make better use of the feedback from the cursor. However, they did not specifically move in a way that maximizes the time the cursor is visible close to the target because there was no significant difference between the time it took the hand to move through the last third of the path in the first and last nine trials with feedback ($t_8 = 0.07$, $p = 0.95$).

In the spatial feedback condition (Figure 2F), subjects moved faster (but did not start moving earlier) as the delay was increased. The difference between the time the movement took (sum of reaction and movement times) in the first nine trials with feedback and in the last nine trials with feedback decreased across trials ($t_8 = 3.64$, $p = 0.006$). Thus, the modest effect that can be seen in Figure 2C is probably the result of subjects having learned to move faster in this condition rather than the result of them having learned to aim farther ahead of the target. Thus, perhaps not surprisingly, the way in which feedback is provided influences how people learn to deal with delays. In the rest of this study we provided feedback by showing the moving cursor throughout the movement on trials with feedback (full feedback) so that subjects explicitly experienced the delay between the hand and the cursor. It is evident that maintaining a constant movement time across trials is not essential for dealing with these delays.

Experiment 2

Having eight combinations of target speed, direction, and initial position ensured that subjects could not simply learn to make a certain movement a certain time after the target appeared. They seem to have learned to aim farther ahead of the target (except in the spatial feedback condition in which they learned to move slightly faster). With full feedback, they seemed to keep the time they reached the target constant and to adjust how much farther ahead of the target they should aim. To determine whether maintaining a constant movement time across trials is essential for dealing with delays, in this experiment we also varied the starting position of the hand.

Procedure of Experiment 2

The second experiment was very similar to the *full feedback* session of Experiment 1, but the starting position of the hand changed randomly across trials. It could be 5, 10, or 20 cm closer to the subject than the target's path (keeping the target's path at the same place as in Experiment 1). We also varied the target's movement direction, speed, and initial position randomly across trials, as in Experiment 1. The variations in the target's motion were independent of the variations in the hand's starting position.

The experiment started with 48 trials with no visual feedback. Then the cursor with a delay of 60 ms was shown for 48 trials. Next the delay increased by 1 ms per trial to reach a total delay of 200 ms. Finally, the delay of 200 ms was maintained for 40 more trials. As in Experiment 1, there was one trial without feedback after every eight trials with feedback. In total, the session consisted of 288 trials and took about 23 min to complete. Nine subjects (seven females) took part in the experiment.

Results of Experiment 2

When starting closer to the target's path, subjects intercepted the target sooner after it appeared. On average, they intercepted the target 714, 795, and 893 ms after it appeared when the starting point was 5, 10, and 20 cm from their path, respectively. The time they took to intercept the target when starting 20 cm from the path (as in Experiment 1) is very similar to the time they took in Experiment 1. Varying the movement amplitude did not prevent subjects from adapting to the temporal delay (Figure 3A through C). The results look more variable than those for the full feedback condition of Experiment 1, but this is mainly because the starting positions of the hand were chosen at random for each trial, so that each point represents a mean of three subjects' values instead of the mean of nine subjects' values. Moreover, one can expect more variability for shorter movement distances because mean movement times are shorter for shorter distances (we found mean movement times of 307, 444, and 581 ms for starting distances of 5, 10, and 20 cm from the target's path, respectively). With less time to complete the movement there is also less time to adjust the ongoing movement on the basis of visual feedback from the cursor, so performance is more similar to that in the late feedback condition of Experiment 1. (We find slightly more variability and slightly less complete compensation for the delays when starting 5 cm from the target's path.) For the shortest starting distance, the movements took less time and the hand moved more slowly when it crossed the target's path. It was moving at 36 cm/s, whereas it was moving at 43 cm/s when starting at a distance of 10 cm and at 49 cm/s when starting at a distance of 20 cm. Moving more slowly could also contribute to the larger temporal variability (Brenner et al., 2012).

Experiment 3

The results of the first two experiments indicate that subjects can learn to cope with delayed feedback even if the movements of both the hand and the target vary across trials. Did subjects altogether adjust their

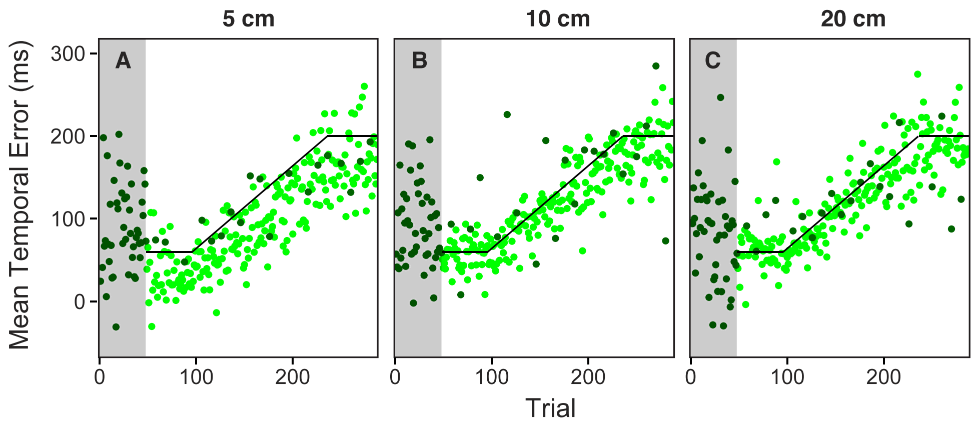

Figure 3. Mean temporal errors in Experiment 2. Each panel shows the data for one of the three movement distances. For further details see Figure 2.

predictions about the hand movements that would arise from motor commands sent to their arm muscles or their predictions about the cursor movements that would arise from their hand movements, or did they specifically learn to move in a certain way to perform a certain task? To find out, we proceeded to examine to what extent learning to cope with delays in one task generalizes to performance in other similar tasks. We started by examining such transfer to a very similar task: passing through a gap rather than through a target. To make sure that the gap was not simply considered to be a different-looking target, we modified the overall task so that subjects had to pass through a static target after passing through the gap. The target was static to ensure that the gap determined the temporal constraints.

Procedure of Experiment 3

On most trials, subjects saw the same moving target as in the previous experiments, with the starting position 20 cm closer to the subject than the target's path (as in Experiment 1). The cursor provided full (delayed) feedback about the movement of the hand. Again, there were some trials without feedback interleaved among the ones with feedback. In this experiment there were also some interleaved trials in which the target was static and 20 cm behind the starting point and a 4-mm-wide, red horizontal bar extended across the whole screen between the static target and the starting position of the hand. The bar was 12 cm closer to the subject than the target. The static target was centered laterally on the surface, at the distance at which moving targets were normally presented. A 4-cm-wide gap in the red bar moved laterally in the same way as the target did in the trials without the bar. Subjects were asked to pass through the gap to reach the static target. They never received feedback when moving through the moving gap to reach the static target.

The session started and ended with blocks of 10 trials in which subjects had to pass through the moving gap to reach the static target. Between these blocks, a sequence of four interception trials with full feedback, one without feedback, four more with full feedback, and one gap trial was repeated 38 times. Gap trials were always performed without visual feedback. The delay increased gradually from 60 to 200 ms, in steps of 1 ms per trial with feedback, and then remained at 200 ms. In total there were 400 trials and it took about 30 min to complete the task. Nine subjects (five females) took part in the experiment.

Results of Experiment 3

We examined transfer from intercepting moving targets to moving through a moving gap to reach a static target. In the latter task, subjects had to pass through a static target, as they did with the moving targets, but since the target was static there were no time constraints involved. The time constraints in these trials were when passing the gap, so we report the temporal errors when passing the gap.

As was expected, subjects learned to deal with the delay when intercepting moving targets. This can be seen by the fact that their mean errors followed the imposed delay, both when the cursor was visible and in the interleaved trials without visual feedback (green disks in Figure 4). The imposed delay had less influence on the temporal errors in interleaved trials in which the hand had to pass through a moving gap to reach a static target (red triangles) than in the interleaved interception trials without feedback, although the tasks are very similar in terms of having to pass a certain place (target or gap) at a certain time. This difference is visible mainly during the early trials of the session. When feedback with a relatively short delay was

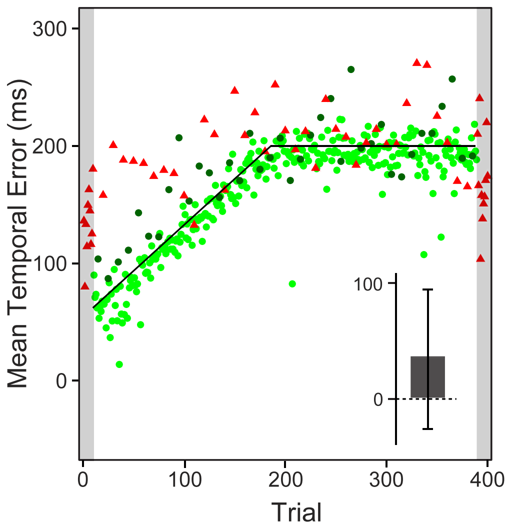

Figure 4. Mean temporal errors in Experiment 3. On some trials (red triangles) the hand had to pass through a gap to reach a static target. Red triangles indicate how much earlier than the center of the gap the hand crossed the point at which it crossed the gap's path (averaged across subjects). No feedback was provided when moving through the gap. For further details see Figure 2.

provided during interception, the temporal error for interception followed the feedback quite closely, but the temporal error for passing the gap remained very high.

Despite extensive training (hundreds of interception trials with feedback), the temporal error when passing through the gap at the end of the session was not significantly different from that at the beginning of the session (right inset in Figure 4; $t_8 = 1.31$, $p = 0.23$). However, this finding does not provide conclusive evidence against transfer because the magnitude of the difference in performance between these blocks is not very different from the magnitude of the difference shown in the inset of Figure 2A. Thus, we cannot be certain that there is no transfer from interception to passing through a gap, but we can conclude that subjects have not generally changed their expectations about the timing of the consequences of their motor commands because the learning is at least partially task specific.

Experiment 4

We did not find complete transfer of learning to deal with delays from intercepting moving targets with a delayed cursor to passing through moving gaps (to reach static targets). Thus, the exposure to the delays had not adjusted the overall predictions about the consequences of motor commands or actions. However, it was not certain that there was no transfer at all, so the transfer may not be completely task specific. To further study the task specificity of the transfer of temporal adaptation, we examined generalization to slightly different conditions within the interception task as well as from interception to manual tracking.

Procedure of Experiment 4

The session started and ended with subjects manually tracking a moving dot with their unseen hand for 30 s. The 2-cm-diameter white dot was initially 10 cm to the right of the center of the tablet. Subjects had to move the hand to this position; once they reached it the dot started moving sinusoidally across the midline of the tablet. It moved at 1 Hz, with a peak-to-peak amplitude of 20 cm, for 30 s. Subjects were instructed to track the target with their unseen hand. The delay (or anticipation) in doing so was determined by fitting a cosine to the positions of the hand and comparing the phase of the fit cosine with that determining the positions of the target. No visual feedback was provided. Between the two tracking episodes, Experiment 2 was repeated, but feedback was provided only for distances of 5 and 20 cm. No feedback was provided when starting to move at the distance of 10 cm from the target's path. The starting position for the interception trials was varied from trial to trial as in Experiment 2. In total, each session consisted of 288 interception trials and two manual tracking tests. The whole experiment took about 25 min to complete. Ten subjects (seven females) took part in the experiment.

Results of Experiment 4

Learning to cope with the delayed feedback when starting 5 and 20 cm from the target's path transferred to movements starting 10 cm from its path (Figure 5). For the latter movements, there was a clear difference between the temporal error during the extended intervals when the delay (that was visible only for the other movement distances) was 60 ms and the temporal error during intervals when the delay was 200 ms (inset of Figure 5B; black bar; $t_9 = 6.04$, $p = 0.0002$; the intervals in question can be recognized by the horizontal line segments). The difference is less than the 140-ms difference between the imposed delays, probably because there is an overall tendency for the hand to arrive too early (positive values of the mean temporal error) when intercepting targets without visual feedback. That the difference is larger here than when comparing performance before and after exposure to delays with full feedback in Experiment 1 (Figure 2A) is probably because these measurements were interleaved with trials with feedback for the other distances. The

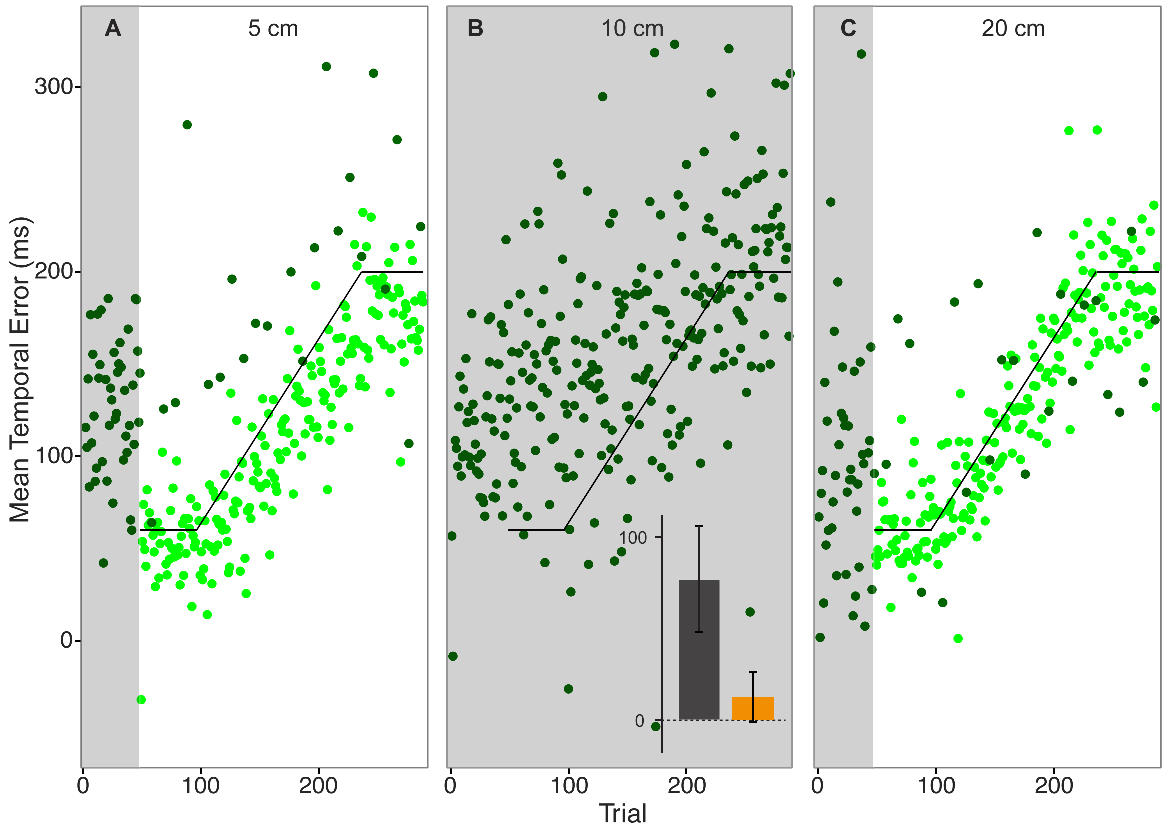

Figure 5. Mean temporal errors in Experiment 4. No feedback was provided when the movement distance was 10 cm. The black bar summarizes the transfer of learning to deal with the delay from trials with movement distances of 5 and 20 cm to trials with a movement distance of 10 cm. The orange bar summarizes transfer to the manual tracking task. For further details see Figure 2.

change in the mean temporal error during the experiment was quite similar for the 10-cm condition as for the trials without feedback in the 5- and 20-cm conditions. There is a lot of variability in the errors for the 10-cm movements, probably partly because ongoing movements cannot be adjusted due to the absence of visual feedback and partly because the starting position of the moving hand changed randomly, so on average each point represents a mean of three subjects rather than 10 (as was the case in Experiment 2).

The orange bar in Figure 5B shows how much less the hand lags behind the target during the last 20 s of manual tracking after the interception task than during the last 20 s of manual tracking before the interception task (we removed the first 10 s of each tracking episode because it took subjects some time to catch up with the target when it started moving and to get into the rhythm). Adapting to the 200-ms delay in the interception task did not influence manual tracking significantly ($t_9 = 1.75$, $p = 0.08$). Again, we cannot be certain that there is no transfer at all, but it is clear that the transfer is modest at best.

Experiment 5

The previous experiments suggest that the extent to which learning to deal with delays transfers to different circumstances depends on the extent to which the task has changed. We found clearer transfer to movements from a different starting position while performing the same task than to movements in different tasks, although those tasks (passing through a gap and manual tracking) share the need to synchronize movements of the hand to external visual stimuli. To determine whether it is the task that is relevant, or similarities between the visual stimuli or between the movements that need to be made, we conducted an experiment in which we examined the transfer of learning to deal with delays between a number of timing tasks. In addition to intercepting a moving target and moving back through a moving gap, we used (a) one task with target motion similar to that of the target that one had to intercept, but in which a different arm movement was required, and (b) a second task that required arm movements similar to those used during interception, but in response to a completely different stimulus.

Procedure of Experiment 5

This experiment had four sessions. The basis of the experiment was the usual interception task, but in order to go back to the starting position subjects had to pass through the bar with the moving gap. The bar with the moving gap had the same characteristics as the bar used in Experiment 3 but was now presented during the return movements and 10 cm closer to the subject than the target's path. In two of the sessions subjects had full feedback during the interceptive movements but no visual information was available during the return movement (except when the hand was static). In the other two sessions, full feedback was available when returning to the starting position (passing through the gap) but not while intercepting the moving target. In both cases there were also interleaved trials without visual feedback.

One of each of the pairs of sessions started and ended with a block of 10 trials and contained interleaved trials in which subjects had to lift their hand to indicate the time of a collision between a moving target and a static bar (similar to the task in Pesavento & Schlag, 2006). The target was selected at random from the targets that were used for the interceptive movements. It moved toward a red, 4-cm line (4 mm width) that intersected the target's path straight in front of the starting point. In the other two sessions subjects had to cross a similar line (at the same position, 20 cm farther from the subject than the starting point, but oriented along what would be the target's path) at the time of the third of a sequence of three tones (onset asynchronies of 500 ms). They started their movements at the same position for all tasks (except passing through the gap during the return movements). No feedback was ever provided for the collision or auditory tasks.

Between the initial and final blocks of 10 trials there were 38 sequences of four interception and return movements with feedback when moving in one of the two directions, an interception and a return movement without feedback, another four interception and return movements with feedback when moving in one of the two directions, and a transfer trial. The transfer trial was either lifting the pen at the time of collision or synchronizing reaching the static target with the time of the third tone. The visual delay in the trials with feedback increased from 60 to 200 ms at 1 ms per trial and then remained at 200 ms. Each session consisted of 408 trials (or 742 trials if we consider returning through the gap as a separate movement). Ten subjects (eight females) took part in the experiment that lasted for about 32 min per session. They performed the four sessions on different days in a counterbalanced order.

Thus, to summarize, there were four sessions in which subjects had to intercept the target and then pass through a moving gap when returning to the starting position. In two of the sessions delayed visual feedback was provided when intercepting the moving target and no visual feedback was provided when moving back to the starting position. In the other two sessions delayed visual feedback was provided when moving back to the starting position but not when intercepting the moving target. In one session of each pair, subjects also sometimes had to reach a static target at the time of the third of a sequence of three tones. In the other session of each pair, subjects sometimes had to lift their hand when a moving target collided with a static bar. No feedback was ever provided in these transfer tasks.

When synchronizing the arrival of the hand at the target with the third tone, the temporal error is how much earlier than the third tone the hand reaches the static bar. When synchronizing raising one's hand with the collision between a moving target and a bar, the temporal error is how much earlier than the collision the stylus (the hand) leaves the tablet's surface.

Results of Experiment 5

When participants had feedback while intercepting the moving target (Figure 6A), their interceptive movements clearly followed the imposed delay (black line) irrespective of whether or not they received feedback on that trial (light and dark green dots). There was no transfer to passing through the gap during the return movements (red triangles). Neither lifting the stylus to indicate when the moving target will collide with the static bar (orange crosses) nor synchronizing the hand's arrival at the indicated position with the third tone followed the delay that was imposed during interception. There was no systematic difference in performance between the blocks of trials before and after the tasks with feedback (Figure 6C: orange bar for lifting the hand at collision, $t_9 = -1.82$, $p = 0.10$; blue bar for synchronization with the third tone, $t_9 = -0.21$, $p = 0.84$; note that transfer of adaptation would give positive values). There does appear to be a slight trend for temporal errors in the interleaved synchronization-task trials to increase as the delay experienced during interception increases. An opposite trend appears to be present for the collision task.

Figure 6B and D show the corresponding results for the sessions in which the delayed visual feedback was provided when subjects were moving back to the starting position through the moving gap. Participants adapted to the imposed delay (black line) for the task for which feedback was provided (passing through the gap, pink triangles), and performance transferred to trials without feedback for the same task (red triangles), but for some reason there was a strong tendency to move too early (a tendency to be too early when there is no feedback is evident for most of our tasks, and has been reported before; Brenner, Cañal-

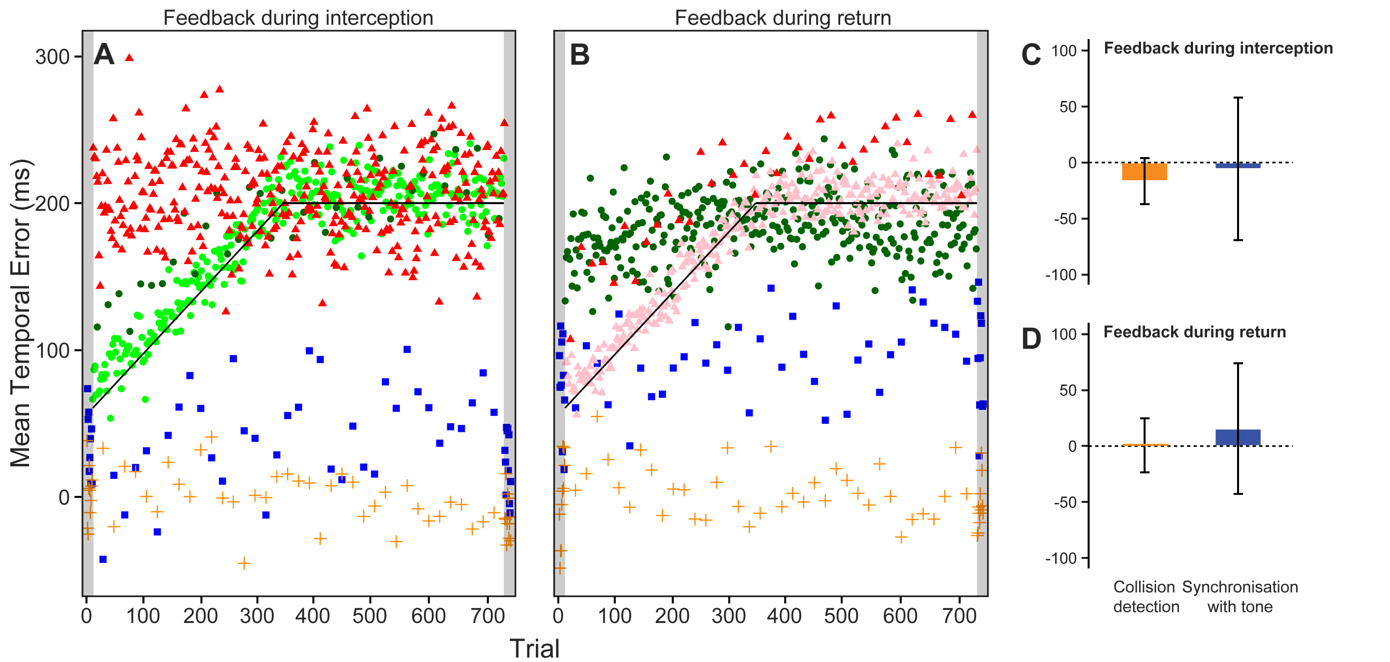

Figure 6. Subjects intercepted a moving target and then passed through a moving gap on the way back to the starting position (Experiment 5). Delayed visual feedback was provided either when intercepting (A) or when returning (B). The green dots represent interception with delayed feedback (light) or without feedback (dark). Passing the gap on the way back to the starting position is represented by pink triangles when there was delayed feedback and by red triangles when there was no feedback. Transfer to lifting the hand when the moving target hits a bar (orange crosses) and to arriving at a static target in synchrony with the third of a sequence of three tones (blue squares) was evaluated both during the session and by comparing performance before and after exposure to the delayed feedback. (C–D) Mean values for the latter comparisons with 95% confidence intervals.

Bruland, & van Beers, 2013). Performance transferred modestly, at best, to interception without feedback (dark green dots). Again, we found a slight trend in the direction that one would expect from dealing with delays when synchronizing arrival at a target with the last of three tones, and a trend in the opposite direction for lifting the hand at the time of the target's collision.

Lifting one's hand to indicate a time of collision is quite different from intercepting a moving target in terms of the movement that is made, but both tasks involve predicting when the target will be at a certain position in space. Arriving at an indicated position (near where moving targets were intercepted) at a time indicated by a tone does not require visual prediction, but does involve making the same kind of movements as interception. In Experiment 1, subjects dealt with the delays by aiming farther ahead of the targets, with a negligible influence on the movement time. The fact that there was no transfer to the collision detection task suggests that this is not because subjects overestimate how far the target will have moved by the time the hand starts moving. The limited transfer to the synchronization task indicates that subjects do not overestimate the time that it will take for their hand to reach the target. It is also worth noting that transfer to the collision detection and synchronization tasks was not stronger when feedback was provided during interception than when feedback was provided during the return movement, although both tasks were designed to include certain aspects of the interception movement: the target's or the hand's motion.

Experiment 6

The previous results seem to indicate that learning to deal with delayed feedback hardly generalizes to other tasks but does generalize to other movements as long as the task is the same as the one in which the delay was experienced. To examine the extent to which transfer does occur within a single task, we examined the transfer from interception when moving away from one's body (as in all previous experiments) to interception when moving back toward one's body, and vice versa. The task was the same for both movements, but the starting position, the direction of the hand's movement, and the position of the target's path were all different.

Procedure of Experiment 6

This last experiment had three kinds of sessions that all combined interception moving away from the body with interception moving toward the body. In all sessions, subjects initially had to move the hand to the usual starting position, and from then on they had to try to intercept moving targets. The first target appeared only when the hand was at the starting position. From then on, new targets appeared 500 ms after the hand either stopped moving or started moving in the opposite direction. The first target was moving at the usual place. Target distance then alternated between being 20 cm closer to the body than usual (at the usual distance of the starting point) and being at the usual distance. As in previous experiments, the target's movement direction, speed, and initial lateral position changed randomly across trials. Since new targets appeared shortly after each interceptive movement ended and targets were intercepted at quite diverse positions on their paths, the movements started at a wide range of positions.

In one session, subjects saw the delayed cursor only when it was on its way to intercept targets moving along the more distant path, so only when the hand was moving away from the body. In a second session, subjects saw the delayed cursor only when it was on its way to intercept targets moving along the nearer path, so only when the hand was moving toward the body. In the third session, subjects saw the delayed cursor when it was moving in both directions. As in all the previous experiments, the delay was increased by 1 ms on each trial with feedback. Trials in which subjects had no feedback were interleaved with trials in which feedback was provided.

Each session started and ended with 20 movements in which subjects had no visual feedback at all, irrespective of the direction in which they were moving. Between these blocks, the cursor was delayed by 60 ms for 40 movements, then the delay increased by 1 ms after each movement in which feedback was provided until the delay reached 200 ms, and finally the delay of 200 ms was maintained for another 36 movements. This procedure meant that there were 432 trials in the two sessions in which feedback was provided when moving in one direction (considering each interceptive movement to be a different trial). These sessions took about 18 min to complete. There were 276 trials in the session in which feedback was provided when moving in both directions. This session took about 10 min to complete. There were fewer trials in this session because feedback was provided when moving in both directions, so the delay increased on almost every trial. In the other sessions, feedback was provided only when moving in one direction, so the delay increased on (almost) every second trial.

Ten subjects (nine females) took part in the first two sessions (feedback provided only when moving in one direction). They performed these two sessions on different days in a counterbalanced order. Six subjects (four females) took part in the session in which feedback was provided when moving in both directions.

Results of Experiment 6

The temporal errors followed the imposed delays on trials in which feedback was provided (light green and pink dots in Figure 7). They also closely followed the imposed delays on interspersed trials without feedback when feedback was provided while moving in both directions (dark green and red dots in Figure 7C). They followed the imposed delays less convincingly when feedback was provided only while moving in the same direction (dark green and red dots in Figure 7A, B), suggesting that the movements in the two directions are not timed completely independently. However, they followed the imposed delay even less when feedback was provided only while moving in the other direction (red dots in Figure 7A and dark green dots in Figure 7B), so having learned to deal with delays does not transfer very well to movements in the opposite direction, although the task is the same (to intercept a moving target).

Comparing the blocks of trials without feedback at the beginning and end of each session supports the idea of partial transfer to movements in the opposite direction (while performing the same task). When feedback was provided while moving away from the body (Figure 7A), its influence on the timing of trials without feedback was about twice as large for movements away from the body (green bar) than for movements toward the body (red bar). Thus, transfer is not complete. However, when feedback was provided while moving toward the body (Figure 7B), the difference between the temporal errors before and after exposure to the delayed feedback was similar for movements toward the body (red bar) and away from the body (green bar), suggesting that transfer was almost complete. Moreover, the influence of exposure to delayed feedback appears to be larger when feedback is provided while moving in both directions than when it is provided while moving in only one direction. Thus, there appears to be some transfer of having learned to deal with delays between the two directions of movement, but such transfer is far from complete.

Having received delayed feedback while moving in one direction does not appear to influence similar interceptive movements in the opposite direction much more than it does passing through a gap when moving in the opposite direction (Experiment 3) or moving in the same direction to synchronize one's arrival with a tone (Experiment 5). Thus, it is conceivable that the transfer is limited to similar movements rather than to a certain task. However, in this experiment the movements varied considerably across trials because each movement started where the previous one had ended. The next target was chosen at random, so some movements remained at one side of the surface whereas others crossed the surface diagonally. The different starting points and paths even increased the variability

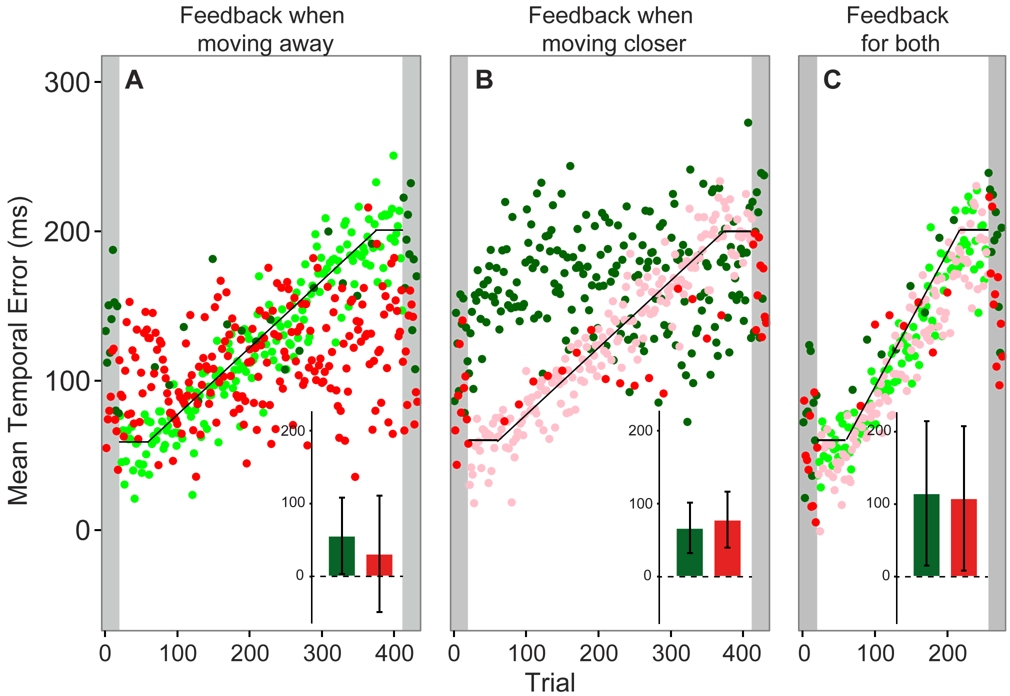

Figure 7. Subjects intercepted targets that were moving at two different distances so that some were intercepted with the hand moving away from the body and others with the hand moving toward the body (Experiment 6). Delayed visual feedback could be provided when the hand was moving away from the body (A), when it was moving toward the body (B), or both (C). The light and dark green dots represent movements away from the body with and without delayed feedback, respectively. The pink and red dots represent movements toward the body with and without delayed feedback, respectively. The bars show the mean differences between the temporal errors before and after exposure to the delays, with 95% confidence intervals. For further details see Figure 2.

in where the targets were hit. The overall mean of the standard deviations in where subjects hit each kind of target is 8.5 cm in this experiment, whereas it was only 3.0 cm in Experiment 1. Thus, transfer is unlikely to be limited to very similar movements. On the other hand, the influence of the direction of movement that we see here is consistent with the larger transfer to moving through a gap in Experiment 3 (movements away from the body) than in Experiment 5 (movements back to the starting point), although the former movements were preceded by an additional movement back to the starting point (without feedback except when the cursor was static). Thus the direction of motion is not unimportant.

The main reason to consider that adjustments to movements toward and away from the body (or toward targets moving along two different paths) might not be completely independent is that there appears to be some transfer in Figure 7B: a gradual increase in the temporal error throughout the session when moving away from the body without feedback (similar gradual increases for the task for which no feedback is provided might be present in Figures 4 and 6B as well). Although this could be the result of a modest amount of transfer, perhaps indicating that multiple mechanisms adapt, the fact that the increase appears to continue seamlessly when (minimally delayed) feedback starts being provided for movements in the other direction (dark green points at the left of Figure 7B) suggests that the increase might just be a continuation of the drift toward an inherent bias when feedback is removed (Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006). Since the feedback is initially delayed less than the inherent bias, any transfer would decrease the errors at that moment rather than giving rise to a continuation of the increase. However, we cannot conclude from this that providing feedback for movements in one direction does not influence movements in the other direction at all because the temporal error decreases rapidly when (delayed) feedback for the same task is removed at the end of the session (Figure 7A, C), which is inconsistent with the inherent bias being so large. What we can conclude is that transfer was far from complete.

Discussion

Sensorimotor adaptation has fascinated scientists for a long time (e.g., Stratton, 1897; von Helmholtz, 1867) and has been studied extensively by visually introducing spatial offsets between the seen and felt position of the hand (e.g., Cressman & Henriques, 2009; Hay & Pick, 1966; Kitazawa, Kimura, & Uka, 1997; Rock, Goldberg, & Mack, 1966; Sarlegna et al., 2003; Smeets et al., 2006) or by mechanically introducing new tools or movement dynamics (e.g., Conditt & Mussa-Ivaldi, 1999; Cothros, Wong, & Gribble, 2006; Shadmehr & Mussa-Ivaldi, 1994). The ease with which people learn to deal with many such manipulations (but see van den Dobbelsteen, Brenner, & Smeets, 2003) becomes evident when we consider the spatial deformations that are introduced by wearing spectacles and the transformations that are required to direct a cursor on a screen by moving a computer mouse with one's hand.

With our increasing reliance on electronic devices we are also regularly exposed to delays between our actions and their sensory consequences. Temporal adaptation has recently been reported for both perceptual and motor tasks (e.g., Cunningham et al., 2001a, 2001b; de la Malla et al., 2012; Heron et al., 2009; Kennedy et al., 2009; Stetson et al., 2006). There are even some reports of transfer across movements or tasks (e.g., Cunningham et al., 2001a; Pesavento & Schlag, 2006).

We examined how people deal with delayed feedback about their arm movements. Since performance was evaluated on the basis of the cursor's motion, points following the black line indicate that full adaptation has taken place, so that the cursor rather than the hand hit the target. Performance was systematically better with full feedback than with late feedback (Experiment 1), probably because ongoing movements were adjusted on the basis of the delayed feedback when possible. Our main interest was in the extent of adaptation to the delayed feedback. Such adaptation is revealed by performance when feedback is provided only once it is already too late to adjust the movement (late feedback condition in Experiment 1), performance in interleaved trials without feedback (in all experiments), and in blocks of trials without feedback at the end of the session (in Experiments 1 and 6).

The adaptation decayed quite rapidly when no more feedback was provided, justifying our choice to include interleaved transfer trials in most experiments. In general, we found more consistent transfer to performing the same task in different circumstances (starting at a 10-cm distance in Experiment 4; moving in different directions in Experiment 6) than to manual timing tasks that differed from the interception task in specific requirements (moving through the gap in Experiments 3 and 5, manual following in Experiment 4, synchronization and collision tasks in Experiment 5). However, the direction of motion made a difference, and we did find some indications of a limited amount of transfer to some of the other tasks in which subjects made similar movements.

Why might the transfer of adaptation depend on the task?

We consider two reasons why the task may be important. The first is that people may learn to deal with the delays by adapting certain judgments so that only tasks for which those judgments are relevant are influenced by the adaptation. Obviously, we would not expect transfer to a task that has nothing in common with the task in which one is exposed to the delayed feedback. That is why we selected transfer tasks that share what we considered to be potentially critical elements of the task in which the delay was experienced. When synchronizing the hand's arrival at an indicated position with the third of three tones (Experiment 5), subjects had to make movements very similar to those that they made when intercepting moving targets. When lifting the stylus to indicate when the moving target will collide with a static bar (Experiment 5), the target's motion was very similar to that of the moving targets that were to be intercepted. When manually tracking the moving target (Experiment 4), subjects had to match the felt position of their unseen hand to the visible position of the target, which is similar to what they must do in the interception trials without (full) feedback. Passing through a gap, either to reach a static target (Experiment 3) or on the way back to the starting point (Experiment 5), is very similar to the interception task in that the hand had to be at a certain place at a certain time. We found little transfer to any of these tasks. We even found that transfer was diminished when moving in a different direction than that in which one had been moving when feedback was provided. Thus, it is not clear what judgment could have adapted. If it is not a judgment that has adapted, the change must be related to the movement or the task.

A second reason why the task may be important is that people may learn to deal with delays in the context of performing specific tasks. They may not generally adapt their judgments or estimates of the consequences of their actions, but specifically learn to perform a certain task in a certain manner. It is not quite clear how one should define a task within this context. The kind of movement that is made may be an important feature because although we find reliable adaptation even if the movement varies considerably across trials (Experiment 6), we saw that the direction of motion can be important, both when intercepting targets (Experiment 6) and when passing through a gap (Experiments 3 and 5). However, it cannot simply be a matter of the direction of the movement because we found very little transfer to synchronizing with the third tone, although the movement that was required was quite similar to that during interception (Experiment 5).

It is important to realize that although the figures show mean temporal errors as if all trials were identical, the experimental design prevented subjects from simply learning to make certain movements. The targets' initial positions, their speeds, and their directions of motion varied across trials. In Experiments 2 and 4 the distance of the hand's starting point from the target's path also varied across trials, and in Experiment 6 the hand's starting position was different for every movement. Moreover, we found transfer to movements for which no feedback was ever given in Experiments 4 and 6. Thus, even if what subjects learned was related to making specific kinds of movements, such learning must generalize to other circumstances for the same task.

We found that our subjects learned how to move their arm to get the cursor to intercept the target. They did not simply learn to make specific movements because we found transfer to different movements. They also did not generally adjust their judgments about the timing of external (visual) events or of how their motor commands influence their actions (or the consequences of those actions) because we did not find complete transfer to any other task. Since the adaptation seems to be task specific, we refer to this as learning to perform a certain task, although the definition of a task remains rather vague.

Previous studies on adaptation and transfer

Most previous studies on temporal adaptation have used discrete rather than continuous tasks or have focused on cross-sensory misalignment (e.g., Fujisaki, Shimojo, Kashino, & Nishida, 2004; Keetels & Vroomen, 2012; Rohde & Ernst, 2013; Stetson et al., 2006). Some transfer of adaptation has been reported for such tasks (e.g., Pesavento & Schlag, 2006), but the mechanisms underlying the adaptation in those studies are likely to be different from those underlying the way subjects dealt with delays in the current study. Kennedy et al. (2009) found adaptation to delayed feedback in a tracking task in which subjects had to synchronize their head movements with flashing lights, and Foulkes and Miall (2000), Miall and Jackson (2006), and Vercher and Gauthier (1992) found adaptation to delayed feedback in manual tracking tasks, but none of them examined transfer to other tasks. Cunningham et al. (2001a, 2001b) adapted subjects to delayed feedback when driving in a simulated street and found transfer to driving in a different simulated street, which is consistent with our observation that what people learn is related to the task rather than to specific movements. Botzer and Karniel (2013) also found transfer between two quite similar tasks: making fast single (reaching) and back and forth (slicing) movements between the same positions. Rohde et al. (2014) adapted subjects to delayed feedback in a manual tracking task and found some transfer to synchronizing hand movements with a sinusoidally moving visual stimulus as well as to judging the relative timing of a flash and a reversal in the hand movement. The latter findings suggest that there can be some transfer across tasks, albeit to very similar tasks because in all cases the hand movements were tracking a visible target or the remembered motion of such a target.

How does one deal with temporal delays?

It is evident from their performance before any visual feedback has been provided (in Experiments 1, 2, 4, and 6) that subjects are quite poor at timing their movements before they have received any visual feedback (also see de la Malla et al., 2012). Subjects learned to deal with the delay best when they saw their whole movement trajectory (full feedback condition), but seeing the part in which the hand crossed the target's path was enough to adapt to the delay (late feedback condition of Experiment 1). From our previous study we know that seeing the cursor pass the target is particularly beneficial for performance (de la Malla et al., 2012), presumably because that is when the temporal relationships are most conspicuous. Seeing the spatial error after each trial (spatial feedback, Experiment 1) was not enough to learn to deal with the delay, probably because without any evidence that the "error" is temporal, subjects mainly make spatial adjustments to the next trial rather than the required temporal adjustments. Making purely spatial adjustments, such as aiming farther to the left if one ended too far to the right on the previous trial because of the delay, does not improve performance because the targets moved in both directions. We did find some temporal adjustment to the delays in the spatial feedback condition: Subjects moved faster. We did not find this adjustment in the other conditions, in which subjects learned to adjust where they aimed.

Rather than aiming farther to one side, subjects may have aimed farther ahead of the target. Aiming a distance ahead of the target is similar to considering a delay, especially if the distance depends on the target's speed. Moreover, it is specific for interception, so if subjects used this strategy it is not surprising that there was no transfer to other tasks such as lifting the hand in response to an impending collision or arriving at a target at the time of the third of a sequence of tones. It is less obvious that it should not transfer to moving through a gap, but gaps might be treated differently than targets (Aivar, Brenner, & Smeets, 2008). Thus, such a task-dependent adjustment could account for our subjects learning to cope with the delays for the tasks for which feedback is provided in our study. Adapting to delays by aiming farther ahead of the target could also explain why adaptation depends on how predictably the target moves (Rohde, van Dam, & Ernst, 2014) because one can reliably aim farther ahead of the target only to the extent that one can know the target's future position.

Concluding remarks

We find that people readily learn to cope with delayed feedback and that such adaptation transfers to new circumstances within what could be considered to be the same task, but does not transfer to completely different tasks. We interpret this to mean that subjects learn to control the item that determines their success within a certain context (here, learning to control the cursor's movements to achieve a certain goal) rather than generally adapting to a changed temporal relationship between their motor commands and the sensory consequences or learning precisely how to move in specific circumstances. Such context-dependent learning could explain why we can so easily learn to deal with various tools, even if they introduce delays. Defining a "task" within this context is far from straightforward, so we are aware that a lot remains to be done before we will really understand why transfer occurs in some cases and not in others. Our results suggest that within this context we will need to specify tasks quite precisely because hitting a target must undoubtedly be considered to be a different task when doing so with a cursor (as in the present study) than when hitting a real ball with a baseball bat.

Keywords: delays, adaptation, transfer, learning, timing, interception

Acknowledgments

This work was supported by grant 2014 SGR79 from the Catalan Government. The second author (J. L. M.) was supported by an ICREA Academia Distinguished Professorship award.

Commercial relationships: none.
Corresponding author: Joan Lopez-Moliner.
Email: j.lopezmoliner@ub.edu.
Address: Vision and Control of Action Group, Departament de Psicologia Bàsica, Universitat de Barcelona, Catalunya, Spain.

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